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Learning and Motivation 36 (2005) 226–244

Learning
and
Motivation

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Episodic-like memory in a gorilla: A review and new findings [☆]

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Received 28 February 2005

Abstract

The current paper examines if gorillas (*Gorilla gorilla gorilla*) possess an episodic memory system. Episodic memory, in humans, is a neurocognitive system that stores information about the personal past. Unique to episodic memory is its palinopsic or past-focused orientation; most memory systems serve to provide the organism with up to date knowledge of the current state of the world. We review four operational definitions that have been used to address issues of episodic memory in non-humans and review the literature with a focus on the studies previously done on gorillas. We describe two new studies with King, an adult male western lowland gorilla. We show that King can remember the order of past events (Experiment 1) and that King can remember where events occurred (Experiment 2). We conclude by discussing alternate explanations of our findings and speculate on future directions.

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[☆] Experiment 2 was conducted as partial fulfillment of the requirement for an Honors' thesis by Megan Hoffman at Florida International University. A full report on this research will be published in *Modern Psychological Studies*, an undergraduate journal. Monkey Jungle and the DuMond Conservancy provided logistical support for the project. We are grateful to Monkey Jungle for access to King and for employees' time. The authors thank Genevieve Tessier for help with Experiment 2. We thank Sharon Du Mond and Steve Jacques of Monkey Jungle for their encouragement, cooperation, and assistance. We thank Tina Casquarelli for her time and expertise. We thank Dr. Ken Gold for permission to reprint the photograph of King.

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doi:10.1016/j.lmot.2005.02.012

Keywords: Gorillas; Episodic memory; Animal memory; Comparative cognition

Introduction

Typically, most research on apes is directed to our nearest genetic relative, the genus *Pan* (chimpanzees and bonobos). Our next nearest relative is the gorilla (*Gorilla gorilla*). Estimates from genetics suggest that the common ancestor of both humans and gorillas lived some 8–10 million years ago (Falk, 2000). Despite this common ancestry, the gorilla is usually overlooked in studies of primate cognition. In this paper, we will review the literature on gorilla memory, with particular attention to issues surrounding episodic memory and temporal cognition. We will claim that gorillas demonstrate a limited episodic memory, that is, an ability to retrieve events from the past. We will first review the literature on episodic memory in non-humans, then review the literature on single-event learning and episodic-like memory in gorillas. Then we will describe two new experiments from our work. We then conclude with some limitations of this research and some directions for the future.

Gorilla cognition has been studied in a number of ways. Investigations have been directed at concept formation (Vonk, 2002, 2003; Vonk & MacDonald, 2002), food processing (Byrne & Byrne, 1993; Pika & Tomasello, 2001), learning (Fischer, 1962; Fischer & Kitchener, 1965; Patterson & Tzeng, 1979; Rumbaugh & Steinmetz, 1971; Yerkes, 1927), linguistic skills (Patterson, 1978), mirror self-recognition (Inoue-Nakamura, 1997; Ledbetter & Basen, 1982; Shillito, Gallup, & Beck, 1999; Suarez & Gallup, 1981; Swartz & Evans, 1994), problem-solving (Robbins, Compton, & Howard, 1978), social cognition (e.g., Maestripieri, Ross, & Megna, 2002; Mitchell, 1991; Stoinski, Wrate, Ure, & Whiten, 2001), and tool use (Fontaine, Moisson, & Wickings, 1995; Nakamichi, 1999). Our focus will be only on issues of memory, especially those relevant to the understanding of episodic memory and mental time travel.

Episodic memory

An event is a unique happening that, by definition, occurs only once. Similar events may occur but because each event is tied to a unique point in time, no two events can ever be identical. Consider the memory of one's college graduation ceremony or a romantic sunset on the beach spent with one's fiancée. One may have spent many such sunsets with one's fiancée but each one is unique in some way. These events are recorded in human memory in a system of memory called episodic memory (Tulving, 1983, 1993, 2002). An episodic memory system is designed to store relevant individual events from one's personally experienced past over long stretches of time. In contrast, semantic memory refers to our knowledge about the world (Tulving, 1983). For example, one may know that Windsor, Ontario is south of Detroit, Michigan, or one may know that the chemical formula of water is H₂O. Indeed, some information in semantic memory may refer to the past, but it is not the personal past (e.g., Julius Caesar was murdered in 44 B.C.).

According to most conceptualizations of episodic memory in humans, it involves a mental model of the past world, or “mental time travel”; that is, an awareness that the retrieved memory refers to a past event (Cabeza, 1999; Tulving & Markowitsch, 1998; Wheeler, 2000). Tulving and Lepage (2000) referred to this past orientation as *palinoscopic memory*. Palinopscope requires the focus of the memory to be on what has passed. For example, I may know that my keys are in the basket by the door (present-focused), but this does not require me to remember the event of placing them there the last time I came home (past-focused). A classic example of palinoscopic memory is eyewitness memory, in which people are required to tell the district attorney what they remember about the witnessed crime. A good witness describes what he or she recalls happening in the past. One can know (semantic memory) that the children stole the cookies by following the trail of crumbs, but one remembers (episodic memory) seeing the children sneak off with chocolate smeared on their faces. The eyewitness describes the latter.

Few studies have directly addressed if animals have memory systems similar to human episodic memory (but see Clayton, Bussey, & Dickinson, 2003; Hampton & Schwartz, 2004; Roberts, 2002 for reviews). Recently, however, there has been a surge of interest in the possibility of episodic or episodic-like memory in non-humans (Clayton & Dickinson, 1998; Clayton, Yu, & Dickinson, 2001; Menzel, 1999; Morris, 2002; Schwartz, Colon, Sanchez, Rodriguez, & Evans, 2002; Schwartz, Meissner, Hoffman, Evans, & Frazier, 2004; Zentall, Clement, Bhatt, & Allen, 2001).

Applying the concept of episodic memory to animal memory is a controversial issue. There is no agreed operational definition of non-human episodic memory (Hampton & Schwartz, 2004). This has led to huge differences in pre-existing assumptions as to the nature of episodic memory in non-humans. On the one hand, there are some commentators (e.g., Donald, 1991; Olton, 1984) who have argued that episodic memory is widespread in the animal kingdom, whereas others (e.g., Suddendorf & Corballis, 1997; Tulving, 1983) have argued that episodic memory is uniquely human. Clearly, these authors are making their claims based on different operational definitions of episodic memory.

Operation definitions of episodic memory

We review four operational definitions of episodic-like memory that have been used in the recent animal cognition literature. Two come from research on birds (i.e., Clayton & Dickinson, 1998; Zentall et al., 2001) and two from research on apes (Menzel, 1999; Schwartz et al., 2004) (for additional conceptions of episodic memory in non-humans, see Eichenbaum & Fortin, 2003; Morris, 2002). Each definition focuses on a different aspect of how the human episodic memory system operates. We will describe each approach, as studied in different species, and then assess how well it addresses the issue of episodic memory.

What, where, and when

Clayton and Dickinson developed criteria, based on Tulving's (1972) original conception of episodic memory, to examine “episodic-like” memory in non-humans

(Clayton et al., 2003; Clayton & Dickinson, 1998, 1999, 2000; Clayton & Griffiths, 2002; Clayton et al., 2001; Griffiths, Dickinson, & Clayton, 1999). According to their view, episodic-like memory stores information about temporally dated events and the spatial–temporal relation inherent in the event. Episodic memories are not of single bits of information; they involve multiple components of an event linked (or bound) together. They sought to examine evidence of accurate memory of “what,” “where,” and “when” information, and the binding of this information, based on a trial-unique learning event.

Clayton and Dickinson (1998) focused their research on food-storing birds, in particular, the California scrub jay (*Aphelocoma californica*). These birds cache extra food in the wild and return to the cache sites later when food is in short supply. Clayton and Dickinson devised an ingenious experiment to determine if jays would act similarly in the laboratory, specifically, if they would remember the location of two items of food that were cached under trial-unique conditions. Their paradigm was based on a jay’s preference for fresh worms over peanuts during short intervals of time and a shift in their preference over time because worms degrade more quickly than peanuts. At the start of each trial, the jays were forced to cache foods in an ice-cube tray. Worms were stored on one side and peanuts on the other side of the tray. After varying intervals of time, the jays were allowed to choose one side of the tray. Clayton and Dickinson showed that jays preferred worms at short-retention intervals and peanuts at long-retention intervals. That is, depending on how long ago the food was stored before testing, the birds’ preference switched from worms to peanuts. These results show that jays not only remembered *what* type of food was hidden, but *when* and *where* it was stored. Of course, previous research demonstrated that food-storing birds remembered what was stored and where (e.g., Kamil, Balda, & Olson, 1994), but Clayton and Dickinson were the first to demonstrate the “when” component as well.

The methodology falls short of addressing the issue of palinopsychy or orientation toward the past. The jays may continually update their knowledge of the world at the current moment and therefore know what food is where and whether it is fresh or not. Updating here refers to some process that adjusts “semantic” or “reference” memory to store the most up to date information. In the wild, this is important for animals because fires burn down trees, predators move to new dens, and trees get picked clean of fruit. Thus, we claim that what the jays are asked to do in this task is more akin to one remembering where one keys are than one remembering who stole the cookies from the cookie jar. Thus, however compelling this research may be, the methodology and the operational definition of episodic-like memory behind it do not accord with a key aspect of human episodic memory, palinopsychy or orientation to the past. Hampton and Schwartz (2004) have also described other shortcomings of this paradigm in addressing the issue of episodic memory.

Surprise test after unique events

The next operational definition comes from the work of Zentall et al. (2001). Their definition is based on tests of an animal’s ability to recall a unique event when it is not expecting a test. Zentall et al. argue that an animal would not attempt to update information when trained on a paradigm on which it did not anticipate a test. Zentall et al.

consider the surprise to be important because it reduces the likelihood of non-episodic encoding processing. They reasoned that if the test were anticipated, the animal could continually rehearse the response until it is reinforced. Rather, Zentall et al. wanted their pigeons to retrieve a past event and report on the relevant information.

To apply this definition, Zentall et al. (2001) trained pigeons (*Columba livia*) to respond to a red light if they had just pecked and to respond to a green light if they had not. This would later serve as the method by which the pigeons could demonstrate memory of an event. The pigeons were then trained to peck when presented with a yellow stimulus and not to peck when presented with a blue stimulus. The two kinds of training were not combined during the pre-test period.

After these responses had been trained, Zentall et al. introduced a novel manipulation. The pigeons were given the opportunity to choose red or green after being presented with blue or yellow. Zentall et al. asked, would the pigeons “comment” on their memory by choosing the appropriate color to indicate if they had pecked or not? The results clearly indicated that the pigeons could reliably indicate whether or not they had pecked by choosing green and red appropriately. The data from eight pigeons also indicated that they were above chance on the first few trials, when the element of “surprise” was still there.

Zentall et al.’s study has one major drawback. Although the pigeons are “describing” the past when they demonstrate their knowledge of whether or not they pecked, it is not clear if they are doing so by retrieving a long-term memory representation. The retention intervals were short enough to fall within the domain of short-term memory or working memory (Bjork & Bjork, 1992; Washburn & Astur, 1998). Thus, it is unclear if the pigeons’ performance is being guided by retrieval from working memory or retrieval from long-term memory, let alone long-term episodic memory. Thus, the Zentall et al. (2001) study provides no conclusive evidence for an episodic-like system in pigeons.

Spontaneous recall

Menzel (1999) investigated memory of unique events in a language-trained chimpanzee (*Pan troglodytes*) named Panzee. The unique symbolic ability of this chimpanzee allowed for the kind of experiment that cannot be done with most animals. Panzee is capable of communicating objects, places, and other information by using a lexigram keyboard (see Beran, Savage-Rumbaugh, Brakke, Kelley, & Rumbaugh, 1998). This allowed Menzel to evaluate Panzee’s ability to spontaneously recall unique events by using particular symbols after long-retention intervals.

In this study, an experimenter hid foods and assorted objects just beyond the fence of Panzee’s outdoor enclosure. Panzee could see the food being placed outside but was moved back inside before she could get the food. The experimenter then left the area and Panzee’s caretakers noted what spontaneous communications Panzee used with them. The caretakers had no knowledge of what was hidden and when it was hidden. They were also blind as to the location of the foods or objects, ruling out cueing from the experimenter. The caretakers noted the lexigrams that Panzee chose to communicate, and the physical gestures that Panzee used to capture the caretaker’s attention and to direct the caretakers to the hidden objects.

At retention intervals as long as 16 h, Panzee indicated both memory for the food type (by selecting the appropriate lexigram) and its location (by pointing in the general direction of where it was hidden). She was more likely to use a lexigram for a particular object during the period in which it was hidden than during control periods during which there were no hidden objects. Panzee was also more likely to elicit help from the caretakers when an object was hidden than when it was not.

Importantly, Panzee remembered both the “what” and “where” components of events that were based on unique events. Furthermore, Panzee’s retrieval of this information was spontaneous, that is, unprompted by any of her caretakers. Panzee’s working vocabulary was about 120 lexigrams, most of which refer to food, and therefore, her use of the keyboard to indicate the hidden item approximates a recall measure. Buchanan, Gill, and Braggio (1981) also used a recall-like measure with a language-trained chimpanzee in a list-learning paradigm. However, the retention interval between the beginning of the learning phase and the beginning of the retrieval phase lasted for a maximum of around 30 s. Therefore, the chimpanzee in the Buchanan et al. study is likely to have recalled from short-term or working memory, whereas Menzel’s data were retrieved from long-term memory. Finally, pointing to food hidden outside Panzee’s enclosure was not a common task for Panzee. Therefore, the trials used also satisfy the trial-unique constraint of episodic memory.

Menzel’s study represents a significant advance in the study of non-human episodic memory, but there is a problem with interpreting Menzel’s results as evidence for episodic memory. The chimpanzee’s memory need not have been past-oriented or palimpsestic. It is possible that Panzee updated her memory about spatial landmarks and their contents and did not need to mentally refer to the event of watching Menzel hiding the food. On this view, retrieval would be based on the present state of the world and not on the occurrence of a past event.

Reporting on past events

Another approach comes from our own work. We have argued that the three main features of episodic memory in humans are long-term memory based on unique events and feelings of pastness when those memories are retrieved (Schwartz & Evans, 2001). The last feature is difficult to demonstrate in non-human animals. As a consequence, we have opted for an operational definition of episodic-like memory in our work with apes that has the following features. The ape’s response must be based on retrieval from long-term memory of a unique event that was learned in a single-trial. In addition, *the animal’s response should provide information about its past rather than about the current state of its knowledge*. This allows us to address the issue of palimpsest or past orientation. One existing task asks animals to report on past events, and that is the delayed match-to-sample task or DMTS (see Hampton, 2001; MacDonald, 1993; Shettleworth, 1998; Washburn & Astur, 1998; Wilkie & Summers, 1982). In DMTS, the animal must report on the stimulus that it just observed by choosing that stimulus from among a set of alternatives. Thus, the animal’s report is of a past event. However, the retention intervals are usually short (usually on the order of seconds), and the event was the last stimulus the animal saw. In our tasks to tap episodic memory, we extend the retention interval beyond that which would be

considered short-term memory in humans (see [Baddeley, 2001](#)). The DMTS task is usually thought of as a test of working memory ([Shettleworth, 1998](#)). Structurally, however, DMTS is quite similar to the methods we have used to examine palinopsia in animals. We now turn to data collected using the “reporting on past events” definition. First, we will describe the gorilla who served as the subject in these experiments.

King is a western lowland gorilla (*Gorilla gorilla gorilla*) who has lived at Monkey Jungle in Miami, Florida, for the last 20 years. At the time we began testing him, King was 30-year old and had a long history of contact and social interactions with his human caretakers. King had received daily enrichment sessions for many years. King shows behaviors uncommon to his species, but only a few of these abilities have ever been studied formally (i.e., mirror self-recognition; [Swartz & Evans, 1994](#); also see [Schwartz, 2005](#)). [Fig. 1](#) shows King at age 32, in his outdoor area.

Previous research

Before formal testing began, King was trained to associate specific cards with specific items of food. Thus, a card with a drawing of an apple on it was associated with both apples and the spoken word “apple.” Five such foods were trained. Because this was done as enrichment by Monkey Jungle trainers, there is no documentation of how many trials and how much time it took King to learn these card/food associations. However, at the start of my research, King was trained to use a particular card



Fig. 1. King, the western lowland gorilla, in his outdoor habitat.

in the presence of each of three different experimenters or when each experimenter's name was spoken. Training continued until King was 90% accurate at presenting the card when either the name was mentioned or the person was present. Ninety percent accuracy was achieved after three sessions (30 trials).

In Experiment 2 of Schwartz et al. (2002), King was expected to make two responses, one about *what* (food) and one about *who*, that is, which experimenter gave King the food. One of two experimenters for whom King had a card gave King a specific food. Retention intervals were either short (5 min) or long (24 h). To be reinforced (with an unrelated food), King had to respond with a card representing both the correct food (the *what* component) and the correct person (the *who* component). King was accurate at both the short- and long-retention interval at identifying both the food (*what*) and the person (*who*) (see Table 1).

In this study, the gorilla's responses were not based on the current state of the world—that is, the food had been distributed and consumed. The response that King made is therefore a reflection on what happened in the past. To be concrete, although King ate an apple at time 1 and the apple is eaten and gone after a retention interval, remembering that action will garner a reward. We rewarded King for the correct answer, which required King to retrieve information about the past. Thus, like Zentall's study, Schwartz et al. showed that the gorilla was referring to a past event. However, unlike Zentall et al., we showed retention at long intervals (up to 24 h).

Nonetheless, this study is not without non-episodic interpretations. First, and most problematic, is that King was tested repeatedly in similar trials. It is therefore possible that he expected the test and that he planned the correct response by encoding the correct food and person “semantically.” He could then rehearse that association (see Washburn & Astur, 1998; for a discussion of rehearsal in non-human primates). Like Panzee, King's responses are potentially guided by semantic as well as episodic memory. Thus, we lack the element of “surprise” that Zentall et al. (2001) consider important. Second, because the tests were five-alternative recognition tests (for food) and two-alternative recognition tests (for people), it is also possible that some responses were guided by the familiarity of the targets rather than retrieval of past events (i.e., Jacoby, 1991; Kelley & Jacoby, 2000). Familiarity here means that the representation of the stimulus was in a higher state of activation, irrespective of how that activation occurred. This compares with recollection in which the stimulus is explicitly associated with an event in the past. However, the 24-h retention intervals suggest that it was not familiarity because the time period would allow activation to

Table 1
King's percent correct (Schwartz et al., 2002)

	Percent correct			
	5-min RI		24-h RI	
	“What”	“Who”	“What”	“Who”
Experiment 1	70%		82%	
Experiment 2	55%	82%	73%	87%

20% is chance baseline for “what” questions; 50% is chance baseline for “who” questions.

decrease, and, in the case of food, King ate many more of the foods from the test set over the course of the day. Thus, other foods may be equally or more familiar to him.

To address some of those issues, we conducted a second series of studies with King (Schwartz et al., 2004), which were based on the human eyewitness memory paradigm. In the study, King witnessed unique events. These events either involved eating novel foods (e.g., sapodilla, cactus fruit, and passion fruit), seeing unfamiliar people or familiar people doing odd things (e.g., stealing a cell phone, doing jumping jacks, and swinging a tennis racket), or seeing unfamiliar objects (e.g., a plastic frog, a baby's shoes, and a guitar). After eating a novel food or witnessing a novel event, King was given a 5- to 15-min retention interval. After the retention interval, three photographs were shown and then given to King. One photograph depicted an aspect of the event (e.g., the object witnessed) and the other two photographs were distractors (e.g., other objects). In another experiment, King had to choose the target person from two incorrect distractors. King's task was to select the correct photograph and pass that card through the bars of his cage to a blind tester. A trainer outside of King's view would then verify if the photograph was the correct one. If it was, King was given food reinforcement.

King's performance in this task was less than stellar (55% accurate overall). However, it was significantly higher than chance (33%). We suspect his performance was weak because some of the photographs might have been hard for him to see and some of the discriminations themselves were difficult (e.g., choosing honeydew over cantaloupe melon). The study does show that King could retrieve unique events from the past based on unique events. Because 24-h retention intervals were not tested, responses based on familiarity could not be ruled out. Thus, we cannot rule out a non-autonoetic response-based familiarity in this study. On the other hand, King's responses are based on past events and not current knowledge, and, in that sense, they satisfy the palinopsy (or past-oriented) constraint.

Schwartz et al. (2004) also examined the misinformation effect. In humans, presenting misinformation about an event after the event has occurred reduces the accuracy of the person's subsequent memory report (see Loftus, 1993; Loftus & Hoffman, 1989 for reviews). This paradigm has been used extensively in eyewitness memory paradigms, a domain of memory which calls on palinopsic retrieval. We wanted to see if King would show the same pattern of interference from misinformation that people do when their episodic memories are interfered with by misinformation.

We again staged events for King, such as an unfamiliar person stealing a cell phone (Schwartz et al., 2004). Five minutes after the event, King was presented with a photograph. This photograph was either in the control condition (blank card), the correct information condition (picture of the actual target), or the misinformation condition (an item related to the correct target). The target could be either the person who performed the event (both familiar and unfamiliar people were used), an object in the event (e.g., the cell phone), or a food given to King (e.g., lychee nuts). Five minutes after the photo was shown to him, King was given cards with which to make a memory response. On the cards were either photographs of three people, three objects, or three foods. In the misinformation condition, one was the correct target and one was the misinformation item. King was only reinforced if he choose the

photograph from the actual event. The results showed that, like with human beings, King's memory performance was impaired by the presentation of misinformation. His accuracy was 53% in both the correct and control conditions, but fell to 40% in the misinformation condition.

In both Schwartz et al. (2002) and Schwartz et al. (2004), we tested what Clayton and Dickinson (1998) would classify as “what” memories. In Schwartz et al. (2002), the target responses referred to food and to people, and in the Schwartz et al. (2004) studies, the target responses were people, food or objects. Thus, if we apply the Clayton–Dickinson criteria of what–where–when memory, King still comes up short, despite his ability to report on past events, not where food is now, as Clayton and Dickinson have done with scrub jays. The current experiments examine if King can represent information about when events have taken place and where events have taken place, while maintaining the criteria that King must respond based on the past rather than learning for the present. Experiment 1 examines the extent to which King can order past events. Experiment 2 examines the extent to which King can comment on where events took place.

Experiment 1: retrieval of the order of events

Experiment 1 examined palinopsis memory for the temporal sequence of three feeding events. Because King was quite accurate at remembering what he ate at both short- and long-retention intervals in Schwartz et al. (2002), we used food as the “event” in this temporal sequencing experiment. In the experiment, King was expected to remember the temporal order of three foods handed to him by an experimenter. This would allow us to see if King has some rudiments of being able to retrieve “when” information from an episodic-like representation. In the experiment, King was required to first respond with a card corresponding to the last food he was given by the experimenter, then respond with the food he had been given second in the sequence, and finally with the food he had been given first in the sequence. We did it in reverse order because when we initially required King to do it in forward order, he always responded with the last food item and grew quite frustrated that he was not getting reinforced for this response (Schwartz, personal observation, May, 2001). Temporal sequencing in memory is an important topic in and of itself (e.g., Terrace, Son, & Brannon, 2003) and recent research has linked temporal sequence memory to episodic-like memory (Fortin, Agster, & Eichenbaum, 2002; Kesner, Gilbert, & Barua, 2002; also see Hampton & Schwartz, 2004).

Method

Subject and stimuli

King was 31-years old when this experiment was conducted. All testing was done in his nighthouse/cage area before he was released onto his outdoor island for the day. The cards which King used to communicate with were the same ones previously

described in Schwartz et al. (2002). Five foods were represented on individual cards (apple, banana, grapes, orange, and pear).

Procedure

An experimenter (in all cases, BLS) gave King a food from the test set. After he finished eating that food, the experimenter waited for 5 min and then gave King another food from the test set. Five minutes after King ate that food, he was given a third food item from the test set. The same food item was not used twice in any given session. Following a 5-min retention interval, the tester (in all cases, trainer TC) would ask him what he ate. Because, in pilot testing, he always responded with the most recently eaten food first, he was reinforced only if he reported the three foods in reverse order, that is input food 3 first, input food 2 second, and input food 1 last. If he was correct on all three foods in the right sequence, he was given a box of raisins as reinforcement by BLS. To be scored as correct, King's responses must be in reverse sequence, that is input food 3 first, input food 2 second, and input food 1 last. Because of vagaries of the trainer's schedule and occasional delays in King's responding, the retention interval varied from 5 to 23 min. King was tested in 30 sessions that were run over 30 different days from May to July 2001.

To compute inferential statistics, we assumed that chance on the first response to be 20% because each food was equally likely to have been presented and he had five cards in his cage with him. However, once King responds to what was eaten on the third temporal order position, it leaves him with a choice of four items to reply to the second temporal order position. Thus, chance for input order 2 is 25%. Likewise, chance for input order 3 is 33%. The binomial test compared King's response to chance performance. These chance probabilities are complicated by the fact that King could, by chance, choose an incorrect item for the third input order item, which was correct for another position. This would then make it impossible for him to get that item correct because we did not replace the cards into his cage if he made an incorrect response. Nonetheless, we assumed that the best model of chance performance was assuming independence on each response.

Results and discussion

King had to respond with the foods he had eaten, and place them in the correct (and reverse order), King was significantly better than chance for all three foods. To be scored correct, King had to respond with the correct food for each input order. He was best for the most recently presented food (input food 3) (90%). However, he was also above chance at input food 2 (50%) and for the first food item (input food 1), 60%. Thus, King was able to remember all three foods and show some ability to correctly order them in time. Although his performance declined significantly from the last food to the second, his performance was significantly above chance for all input orders.

Because King was not only capable of remembering all three feeding events, but reporting them in the reversed but correct order, we argue that King has an ability to order past events in time. We argue that this ability to report on past events and do it

in sequence suggests an episodic-like organization of events (e.g., Eichenbaum & Fortin, 2003). Moreover, since these feeding events are in the past and King is not reporting on where to find food now, we argue that this experiment also illustrates palinscopy or past-oriented memory.

Experiment 2: retrieval of where an event occurred

Experiment 2 examined palinscopic memory of where a unique event had occurred, after long-term memory retention intervals. Because King was accurate at remembering both the “what” and “where” components of unique past events, the hypothesis was that King would be able to remember the “where” component of unique events and communicate this memory by handing the tester the photo card of the appropriate location (see Hoffman, 2004, for a complete description of this experiment).

Method

Subject and stimuli

King again served as the subject. He was 33 when this experiment was conducted. At the time of test, King was given photographs of all three locations and could communicate where the event had occurred by handing a photo card back to the tester. The photographs were taken from King’s perspective inside the nighthouse/cage. The photographs measured 8.89 cm (3.5 in.) × 12.70 cm (5 in.) and were mounted behind acrylic panels, on wooden cards measuring 20.32 cm (8 in.) × 13.97 cm (5.5 in.) × 3.81 cm (1.5 in.).

Procedure

The experiment was conducted on an average of 2 days per week during the months of March through May of 2003. An average of three trials were run on each day of testing. A total of 60 trials were completed, with 20 trials at each of the three locations. The trials were randomized, so that neither King nor the tester could predict the event location on any given trial.

An event was presented at one of three distinctive stimulus locations surrounding the indoor/outdoor enclosure: the main cage, the nighthouse, or the tunnel gate. Testing for memory of the event location was always done in a separate area of his cage because it was removed from the three locations. During both the presentation and testing phases of the experiment, King had access to the entire indoor/outdoor enclosure (the main cage, test cage, and nighthouse), and could move to another area if he did not want to participate in the experiment.

Presentation phase

King witnessed a novel event, performed by a familiar person, at one of three distinct locations: the main cage, the nighthouse, or the tunnel gate. The novel events included such things as watching an experimenter put on a monkey mask and watching an experimenter blow bubbles. On some trials, King was given a small amount of

fruit as an incentive to come over to the event location. The event lasted ≈ 1 –2 min. To ensure that the tester was experimentally blind and unable to cue King to the correct answer, the tester was kept out of view of the three stimulus locations during the presentation of the event. After the event was completed and King had left the location where the event had occurred, an experimenter timed and recorded any visits King made to the other two distractor locations (the two stimulus locations where the event was not presented) or any subsequent visits he made to the event location.

Testing phase

Five minutes after the event had been completed at the event location, the tester was asked to test King. However, because one of the testers was King's primary trainer, she was not always available to test exactly after the 5-min retention interval. The retention interval ranged from 4 to 17 min, with 6 min being the average. Before testing King, the tester was asked to select the location where he/she believed the event had occurred. This was done to investigate if there was a correlation between the tester's choice and King's response (i.e., whether the tester was inadvertently cueing King to the correct answer). The tester was either author BLS or the trainer TC. Neither tester was significantly above chance in selecting the target, and there was not a correlation between the tester's choices and King's choices.

The tester then entered King's testing area and asked King to come over. Then, the tester asked King, in English, where he had seen the familiar person perform the unique event. The tester showed King each of the three photo location cards, and placed the cards between the bars of the cage. King was asked to take the cards and make a response. Handing a card back to the tester was scored as a response only if King had taken all three cards into his cage, so that he could see all of the cards before making a decision. If King made a response before doing this, the cards were replaced between the bars and he was asked to make a selection again.

After King made a response, the tester called out King's response to an out of view experimenter, who then indicated to the tester whether King was correct or incorrect. When King was correct, he was given a food reward (an orange, banana, apple, or grapes) when the tester was BLS or verbal praise from the tester when the tester was TC. King was asked to return the location cards to the tester. If another trial was scheduled for the day, the tester would leave the testing area and another event would be presented. The average interval between the time when an event was tested for, and the time when the next event was presented was an average of 6 min.

The binomial test was used to determine whether King's responses differed from what would be predicted by chance. Because King had three location cards to choose from, chance performance was assumed to be 33%.

Results

King chose the correct location on 27 of 60 trials, for an overall accuracy of 45%, which was significantly above chance using the binomial test, $p < .05$. Although King's overall rate of accuracy was significantly above chance, King exhibited a decline in performance throughout the experiment, showing significantly above

chance performance (60%) during the first 20 trials of the experiment, but declining to chance performance (38%) during the last 40 trials of the experiment.

Analysis of movements during retention interval

Trials in which King visited distractor locations after leaving the event location were analyzed, in order to determine whether visiting a distractor location interfered with King's ability to remember the location where the event occurred; that is, whether King experienced retroactive interference. On 20 of 60 trials King visited distractor locations after leaving the event location. On 17 of these trials King visited just one distractor after leaving the event location. On two of the trials King visited a distractor location and then revisited the event location. And on one trial King visited two distractor locations after leaving the event location. On the trials in which King visited one or more distractor locations, King chose the event location 45% of the time, the recently visited distractor location 25% of the time, and an unvisited distractor location 25% of the time. On the only trial in which King visited two distractor locations, he chose the event location, despite the fact that he had visited all three locations. It appears that King's performance was not affected by visits to potential event sites after the actual event.

Discussion

King's performance was very poor in this experiment. Elsewhere we have speculated as to why he did so poorly in this study (Hoffman, 2004). Here we simply state that he shows some evidence, however inconclusive, of being able to remember where an event occurred. His performance at remembering the location of an event was above chance, statistically, if just barely. His performance was not affected by visits to other potential event sites after the to-be-remembered event ended.

We think this conclusion is bolstered by the findings of MacDonald (1994) and Gibeault and MacDonald (2000), who also found that gorillas could remember locations based on single-trial learning. MacDonald (1994) examined spatial memory in two Western lowland gorillas in the Toronto zoo. In the first experiment, MacDonald set up eight containers in the daytime yard of the adult gorilla. All of the containers initially held food to familiarize the gorilla with the procedure. This conditioned the gorilla to inspect these containers for food. Once the experiment began, however, four sites were baited during two separate phases. During the *search phase* of a trial, four sites were baited. The gorilla was then allowed access to the yard and could search for the food. The gorilla visited each site and removed the food from the container that held food. The gorilla was then removed from the yard. While the gorilla could not see the yard, the same sites that were baited during the search phase were again baited. At some interval later, the *re-search* phase began. During this phase, the gorilla was again released into the yard. The gorilla could minimize the time spent re-searching for the food by only visiting those sites that he remembered as being baited earlier. After the gorilla had obtained the food, a new trial began. In the next trial, four of the eight containers were again randomly chosen to be baited for both the search and re-search phases.

The adult gorilla mastered this task (MacDonald, 1994). He visited baited sites more than unbaited sites up to 48 h following the search phase. Moreover, he consistently terminated his search after finding the four food containers, indicating that he remembered the last configuration of baited sites and how many sites were baited (he stopped after finding the fourth food). Therefore, he recalled both the quantity and the location of the food sources based on a single exposure, up to 2 days later. Thus, the gorillas could retrieve information about the where component of an event that had only been experienced once. MacDonald (1994) conducted a second experiment, with a 1-year-old gorilla. It was similar except that the delay interval between the search and re-search phases was started at 30 s and gradually increased to 10 min. The infant, like the adult, showed above-chance memory concerning where the hidden food was located in the yard.

Gibeault and MacDonald (2000) examined spatial memory in other gorillas at the Toronto Zoo. In this study, they were able to test a larger sample of gorillas. Eight of sixteen sites were baited with food, similar to the search phase of the MacDonald (1994) study. In MacDonald's previous study (1994), when a baited site was visited during both search and re-search, the gorilla dislodged the containers during the visit, and it was obvious later that the site had been visited. Therefore, the gorillas did not have to remember that the site had been visited. However, Gibeault and MacDonald constructed the containers so that the gorillas could remove food from the container, but it would not be obvious, that is, the container looked the same before and after the food was removed. Therefore, the gorillas in the Gibeault and MacDonald study had to remember which containers they had visited.

Gibeault and MacDonald (2000) released two gorillas simultaneously into the yard in order to test if gorillas would compete for the food sites. The test of competition is not relevant here, but what is of interest is if the gorillas avoided previously visited sites—both ones that they had visited and ones that their partners had visited. The results supported single-trial learning of the where component. The gorillas first visited sites during the re-search phase that had been baited during the search phase. All of the gorillas tested were able to avoid visiting already-visited sites, suggesting that the gorillas remembered which sites had been visited.

From our perspective, these studies demonstrate two of the three criteria to demonstrate episodic-like memory. First the gorillas were demonstrating single-trial learning. Second, the gorillas were retaining information based on single-trial learning for over 24 h, clearly within the domain of long-term memory. However, the MacDonald studies do not show palinopsis memory. The gorillas were only required to remember the location of where food was hidden and not necessarily retrieve a representation of finding the food during the search trial.

General discussion

In this paper, we presented a view of episodic memory as it applies to non-humans. We argue that there are three important criteria that animals must pass in order to be classified as possessors of an episodic memory system. First, they must be

able to retain information based on trial-unique (i.e., single-trial) learning. Second, they must be able to maintain this representation over retention intervals that can reasonably be considered within the domain of long-term memory (but see Hampton & Schwartz, 2004; for problems with this view). Third, the animal must be able to demonstrate that it is retrieving a memory of the past event, not simply that it has learned where something is based on a single trial. Thus, the animal's memory must be palinscopic, that is, oriented towards the past.

We have tested King, a western lowland gorilla, for the last several years, for evidence that perhaps gorillas, like humans, possess episodic memory. In two published series of studies, we have shown that King can remember aspects of an event that took place up to 24 h earlier (Schwartz et al., 2002, 2004). These include foods eaten, people who fed him, people who performed unusual events (e.g., playing a guitar), and objects witnessed (i.e., a Frisbee). Because his responses reflect what took place in the past, rather than where things are now, we argue that it is possible his memory responses are based on some form of retrieval of past events, which we call, following Tulving and Lepage (2000) palinscopic memory.

We presented two new studies in this paper. In Experiment 1, we showed that King ordered past events, if in a somewhat limited way. He was able to recall three foods eaten and correctly sequence them in time. In Experiment 2, we also showed that he was capable of remembering where events took place, even though his overall performance was quite poor. Unlike Clayton et al. (2001), we have not combined what, where, and when responses into a single experiment. Note, however, that Clayton et al.'s birds have to peck at a location in a ice-cube tray to indicate their response. That they remember what, when, and where is inferred from their ability to discriminate where the desirable food is. King, however, is communicating a response, in at least one case, symbolically about what he witnessed (or ate) at an earlier time. Reinforcement occurs if he is correct, but the reinforcement is separate from the memory, whereas in Menzel's (1999) study with chimpanzees or Clayton et al.'s experiments, the reinforcement is confounded with memory response. Thus, we think we have demonstrated an element of episodic memory not previously shown.

There are limitations to our findings. King is not able to recall information the way a person can. All of his responses are based on a form of recognition. He examines the cards or photographs and then passes a response to the experimenters. In human memory, we know that relative to recall, recognition is more likely to be based on familiarity processes which need not be episodic in nature (Jacoby, 1991; Kelley & Jacoby, 2000). Familiarity, here, means that one of the target answers somehow looks more salient or is processed more fluently. Thus, a response based on familiarity is not palinscopic in nature because the initial event need not be retrieved. Recall is more likely to be based on recollective processes (Gardiner & Java, 1991), which are palinscopic by definition. We have yet to determine how we could work around this issue with King because he lacks the ability to recall because of the limitations of the communication system developed for him. We look forward to when some of the experiments conducted above can be replicated in a recall format with a language-trained gorilla or chimpanzee.

We make no claims about how King uses these representations of past events in any functional sense. In humans, episodic memories are an integral part of the

autobiographical system which functions to control our conscious sense of self (Conway & Pleydell-Pearce, 2000). Elsewhere we (Schwartz & Evans, 2001) and others (Clayton et al., 2003; Metcalfe & Kober, 2005; Tulving, 2002) have speculated as to the functional value of an episodic system to non-human animals. But, to date, there is no headway in demonstrating the function of being able to retrieve palinscopically. Thus, the jury has still not reached a verdict in the study of episodic memory. We fervently seek evidence that will sway the jury (one way or the other) to reach a truthful verdict.

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